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Sodium accumulation in serpentine and non-serpentine populations of the milkweed Asclepias fascicularis : a thesis ...

Paul N. Thomas
University of the Pacific

Sodium Accumulation in Serpentine and Non-serpentine Populations of the Milkweed *Asclepias fascicularis*

A Thesis

Presented to

the Graduate Faculty

of the

University of the Pacific

In Partial Fulfillment

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Master of Science

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by

Paul N. Thomas

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Paul Norman Thomas

is approved for recommendation to the Committee on Graduate Studies, University of the Pacific.

Department Chairman or Dean:

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Chairman

Dated

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INTRODUCTION

> "All physiological performances of plants, including nutritional ones, are a function of their innate genetic constitution and of the environment in which they live. The interplay between these two factors in the nutritional physiology of plants is especially fascinating because of the great diversity of soil, the main mineral medium of higher plants" (Epstein, 1972: 7).

Serpentine areas with their sparse chaparral vegetation are readily distinguishable from adjacent areas of non-serpentine origin supporting a more lush vegetation. Serpentine rock is rich in ferromagnesium minerals, predominantly $(Mg,Fe)_2SiO_4$ (Proctor & Woodell, 1975). Hydrothermal alteration of this rock produces significantly greater concentrations of magnesium, nickel and chromium than non-serpentine soils. Serpentine soils are usually deficient in nitrogen, calcium, phosphorus and molybdenum. Serpentine soils are characterized by a shallow soil mantle, gravelly texture, low clay content and often occur on steep slopes (Walker, 1954). All of these factors contribute to decreases in moisture and nutrient levels.

The unique ionic characteristics of serpentine soils represent a harsh environment for most plant life. Although there is no single factor which is most critical for determining plant growth on all serpentine soils, the unfavorable Ca/Mg ratio (low calcium and high magnesium) is frequently mentioned (Proctor & Woodell, 1975). One of several mechanisms plants may use to survive on serpentine soils is selective absorption of calcium to ameliorate the toxic effects of excess magnesium (Epstein, 1972).

The requirement for sodium is universal in animals, but not

plants. Sodium in animals helps to maintain the acid-base balance of the organism, is largely responsible for the osmotic pressure of the extracellular fluids, and is critical to many ionic movement and metabolic functions.

The utilization of sodium in vascular plants is rarely discussed. Literature on plant physiology and nutrition either avoids the topic of sodium or limits its discussion to rare examples of halophytic plants. One study (Boyko, 1980) suggested that the milkweed species, Asclepias fascicularis Dene. in A. DC., accumulates sodium from serpentine soils and implied that this species may be using sodium to ameliorate magnesium toxicity.

Because A. fascicularis is found on both serpentine and non-serpentine soils in California and because it was reported to accumulate sodium, this study was initiated to establish the degree of accumulation of this ion in these two soil types. Two other species, Asclepias speciosa Torr. and Asclepias cordifolia (Benth.) Jeps. were included to determine if this characteristic of accumulation occurs in other members of this genus.

METHODS AND MATERIALS

Sample Collection

Stem leaf and flower portions of three species of native California milkweeds and samples of the soil on which they were growing were collected from seven non-serpentine sites (sites 1-7) and eight serpentine sites (sites 8-15) (Fig. 1). Each site represents an area less than $50m^2$. Six separate plants and the soil directly beneath the plants were collected from each site. Species collected were Asclepias fascicularis, A. speciosa, and A. cordifolia (Appendix). All plants were collected while in bloom to facilitate identification. (Identifications were verified by Dr. Dale McNeal, Department of Biological Sciences, University of the Pacific, Stockton, California.)

The entire aerial portion of each plant was collected. Immediately after collection any adherent dust was removed by shaking. Then the stems, leaves and flowers were air dried at 25-30 degrees Celsius for 90 days. The dry plant tissue was next pulverized into a coarse powder in a blender, ground to a fine powder by mortar and pestle, and stored in tightly sealed polypropylene bottles.

Before collecting the soil beneath each plant, the leaf litter, surface roots and rocks were removed to a depth of 2-3 cm. Soils taken included approximately equal amounts from all depths to 25 cm. Soil samples were air dried at 25-30 degrees Celsius for 90 days. The dry soil was then ground to a powder of 20-30 mesh and sifted through a 32 mesh screen (U.S.A. Standard Testing Sieve meshes) to remove pebbles. (This grinding and sifting was done by Mr. Jack Schimasaki of Nelson Laboratories, Stockton, California.) Powder soil samples were then stored in polypropylene bottles.

Figure 1. Map of plant and soil collection sites in California.

Non-serpentine

1. Asclepias fascicularis. 0.1 miles west of Pacific Avenue on the corner of Rivara and Meadow in a vacant lot in Stockton, San Joaquin Co.

2. A. fascicularis. On H Street (Highway 33) at the junction with Overland Avenue north of Los Banos, Merced Co.

3. A. fascicularis. On Highway 152 6.6 miles east of the junction of Highway 152 and Highway 156. Santa Clara Co.

4. A. fascicularis. At the junction of Highway 26 and Highway 12. Calaveras Co.

5. A. fascicularis. 8.8 miles west of Interstate 5 on Del Puerto Canyon Road (Highway 130). Stanislaus Co.

6. A. speciosa. Beside Highway 12 0.1 miles northwest of its junction with Highway 49, north of San Andreas. Calaveras Co.

7. A. cordifolia. 2.3 miles east of Long Barn on Highway 108 on volcanic soil. Tuolumne Co.

Serpentine

8. A. fascicularis. 0.1 miles south of the north fork of the Calaveras River on Highway 49 by drainage ditch. Calaveras Co.

9. A. fascicularis. 1.8 miles on Redhills Road (Sims Road cont.) south of Highway 120 between Yosemite junction and Chinese Camp. Tuolumne Co.

10. A. fascicularis. 2.2 miles east of Frank Rains Park on Del Puerto Canyon Road (Highway 130). Stanislaus Co.

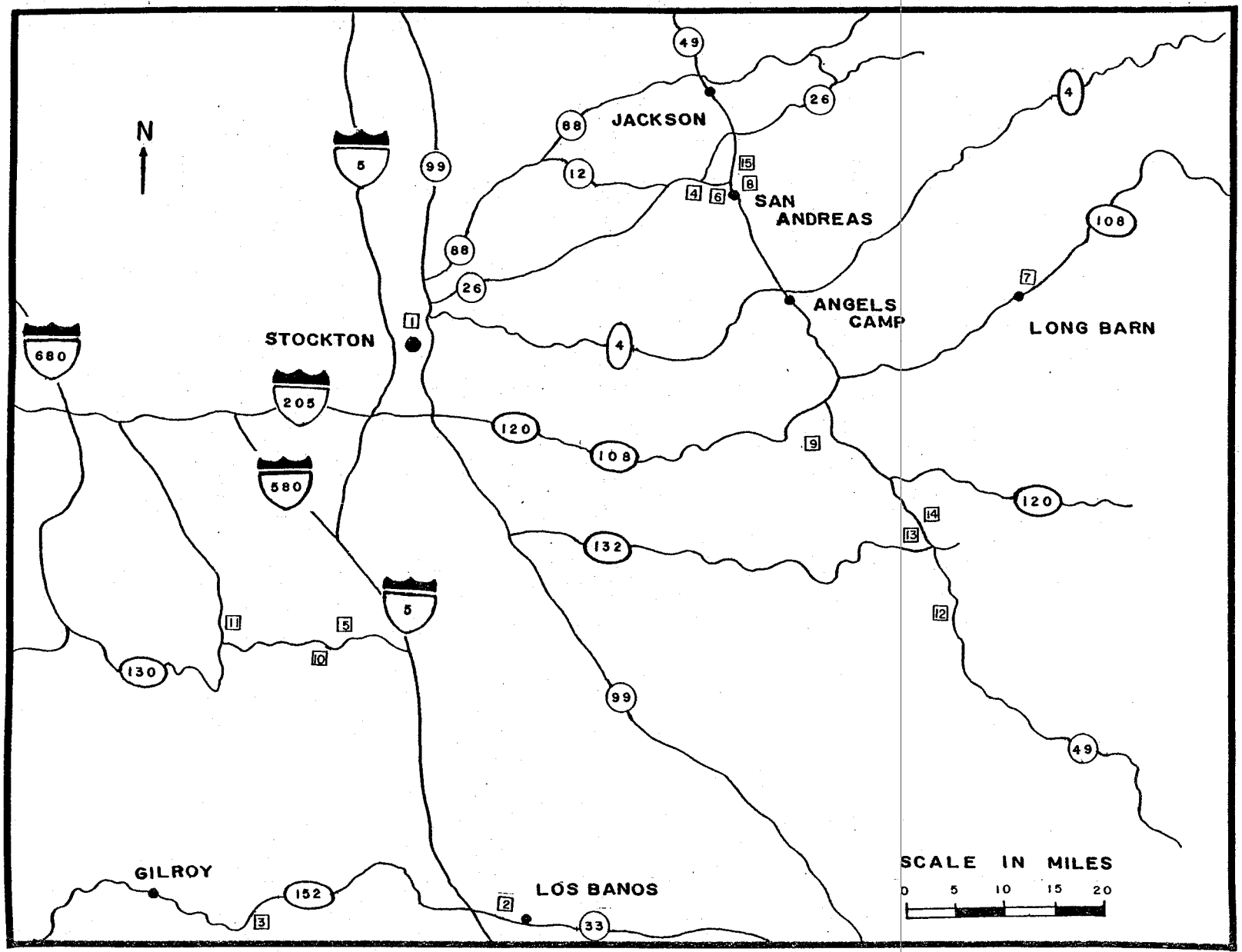
11. A. fascicularis. Off Del Puerto Canyon Road 1.0 miles north of the San Antonio junction toward Livermore. Santa Clara Co.

12. A. fascicularis. 2.1 miles north of the Merced River on Highway 49. Mariposa Co.

13. A. fascicularis. On a side road off Highway 49 1.3 miles south of Mariposa-Tuolumne County line. Mariposa Co.

14. A. fascicularis. 1.2 to 1.5 miles north of the Mariposa-Tuolumne County line on Highway 49. Tuolumne Co.

15. A. speciosa. On Highway 49 at the north fork of the Calaveras River upstream of the bridge. Calaveras Co.


N
JACKSON
SAN ANDREAS
ANGELS CAMP
LONG BARN
STOCKTON
GILROY
LOS BANOS
SCALE IN MILES
0 5 10 15 20
49
26
88
12
99
5
4
6
8
15
108
7
1
680
205
580
120
9
14
13
132
12
11
10
130
33
152
3
2

Plant Analysis

Six one gram samples of dry powdered plant material from each site were placed into clean, dry, pre-weighed crucibles, (all weighings were done on a Mettler, model H15 balance), and ashed according to the method of Johnson and Ulrich (1959). This method requires adding enough of a solution of 5% sulfuric acid in 95% ethyl alcohol to each crucible to saturate the dry material and then igniting the mixture with a bunsen burner to produce a preliminary ash. The sulfated ash has less tendency to fuse to the crucible, thus preventing the loss of some of the elements.

Each sample was then placed in a cold electric muffle oven (Blue M, Muffle Furnace; Model No. M15A - 1A) and heated to 500-550 degrees Celsius for six hours. After the formation of a carbon-free ash of uniform light grey color, the crucibles were removed from the oven, cooled and weighed.

The ashed material was next moistened with a small amount of deionized water (4-5 drops) and 5 ml of 3N hydrochloric acid added. The acidic ash solution was poured into 50 ml Erlenmeyer flasks and the crucibles rinsed with 20-30 ml deionized water to ensure that no ions remained on the crucible walls. The Erlenmeyer flasks then were warmed on a steam bath for approximately 30 minutes to ensure that all salts except silica were in solution. After heating, the solutions were filtered (Watman #1) into 50 ml volumetric flasks, cooled to room temperature, and brought to 50 ml by adding deionized water. Solutions were then stored in airtight polypropylene bottles as the stock solutions for sodium analysis by atomic absorption.

Soil Analysis

Six one gram samples of powdered soil from each site were weighed and placed into 50 ml Erlenmeyer flasks with boiling chips and 15 ml of aqua-regia (3 parts concentrated hydrochloric acid to 1 part concentrated nitric acid). This solution was boiled slowly for about one hour to a volume of 3-5 ml. After cooling, 35-40 ml of de-ionized water was added and the solution boiled for 15 minutes, cooled and centrifuged at 2000 RPM for 8-10 minutes. The liquid portion was then poured into a 50 ml volumetric flask, brought to 50 ml, and stored in airtight polypropylene bottles as the stock solutions for sodium analysis by atomic absorption.

Atomic Absorption

Analysis was done by atomic absorption spectroscopy (Perkin-Elmer, 303) with the machine set at slit 4 and the wavelength at 584.8 nm. Standard dilutions were made from S/P Sodium standard S7385-11. Dilutions (usually 1:19) of the experimental stock solutions were run to obtain absorption values in the linear range of the instrument (0.1 to 3.0 PPM).

Statistical Analysis of Results

Data were analysed using the SPSS package on a Burroughs 6700 computer at the University of the Pacific. The following SPSS subroutines were used: Anova, Oneway, Breakdown, Scattergram and Student's t-test. Unless otherwise stated, significance was determined at the 0.05 level.

RESULTS

A. Asclepias fascicularis

Mean soil sodium concentration in non-serpentine sites is not significantly different from that of serpentine sites (Table IA). There was significant difference in soil sodium between some sampling sites at the 0.1 significance level (Table II). The degree of variability in soil sodium concentrations within sites is shown in Table III.

Mean plant sodium in non-serpentine sites was significantly higher than in serpentine sites ($p<0.002$). Plant sodium varies within non-serpentine and serpentine sites (Table III).

In specimens collected from both non-serpentine and serpentine soil, the concentration of sodium in plant tissue was significantly greater than in soil (Table IV).

In non-serpentine soil the concentration of sodium in the plant was not significantly correlated ($r = -0.18$) with the concentration of soil sodium (Figure 2). In serpentine soil the concentration of sodium in the plant was significantly correlated ($r = 0.80$) with the concentration of soil sodium ($p \approx 0$; Figure 3).

When analysis is restricted to soil sites in which there is no significant difference in soil sodium there is no apparent pattern to plant sodium concentration (Table II).

B. Asclepias speciosa

Mean soil sodium concentration in non-serpentine sites was significantly lower than in serpentine sites ($t = -10.1$).

Mean plant sodium concentration from the non-serpentine site is not significantly different from the serpentine site. Standard

deviations within each site are shown in Table III.

In specimens collected from both non-serpentine and serpentine soil, the concentration of sodium in plant tissue was significantly greater than in the soil (Table IV).

C. Asclepias cordifolia

The mean soil sodium concentration at site 7 (29.8) is significantly higher than all other sites (Table III). The standard deviations for plant and soil variability within site 7 are given in Table III.

The concentration of sodium in the plant tissue at this site was significantly less than in soil (Table IV).

D. Comparison between species

Both Asclepias fascicularis and A. speciosa accumulate sodium in both serpentine and non-serpentine soil. A. cordifolia excludes sodium in non-serpentine soil. Accumulation of sodium is significantly greater in A. fascicularis than in A. speciosa in both serpentine and non-serpentine soil (Table IV).

DISCUSSION

All vascular plants show some selection in the uptake of substances from soil by accumulation and exclusion of specific ions. Most ions considered essential for normal plant development (Ca, Mg, K, etc.) are accumulated by plants. Substances which are not required for normal plant development, but are in high concentrations in the soil, may be selectively excluded by plants (Epstein, 1972). Magnesium exclusion by non-endemics on serpentine soil is necessary to keep plant magnesium concentrations below toxic levels (Proctor & Woodell, 1975).

Although sodium is not generally required by vascular plants, most organisms, regardless of their phylogenetic origin, require sodium. Several groups of bacteria are halophilic and cannot grow except in the presence of high concentrations of sodium chloride (Epstein, 1972). Many marine algae accumulate salt to prevent plasmolysis and sodium has been shown to be essential for the blue-green alga Anabaena cylindrica (Allen & Arnon, 1955).

Many species of Phycomycetes, Ascomycetes and Fungi Imperfecti are found in marine environments and their reproductive stages require sea water (Hellebust, 1976).

Certain halophytes (salt plants) which are indigenous to saline soils not only tolerate the high salt concentrations but actually require sodium. Brownell discusses the necessity of sodium for the growth of the bladder salt bush Atriplex vesicaria (Brownell, 1965) and Williams (1960) found the salt requirement of Halogeton glomeratus (28.6% of its dry weight is sodium) so high that sodium may be considered a macronutrient element for this species.

Halophytes growing in highly saline soils require a relatively high salt content for two reasons. First, they must maintain a balance between cations and anions. For example, Halogeton glomeratus produces a considerable amount of oxalic acid and needs large amounts of sodium to maintain a charge balance (Williams, 1960). Secondly, plants must combat the low osmotic potential of saline soils and accumulate sodium ions to maintain turgor (Hellebust, 1976).

Most halophytic species have developed specialized means of accumulating sodium in a way which won't be toxic to the plant. Desert shrubs of the genus Tamarix excrete sodium from salt glands in the leaves (Epstein, 1972). The bladder salt bush, Atriplex vesicaris, stores sodium in epidermal bladder cells and many species have increased succulence as sodium levels increase (Brownell, 1965).

To be accumulated any ion must be available by being in solution. Soils release mineral elements by the dissolution of soluble salts and by ion exchange (mainly cation exchange). Cation exchange is the transfer of cations from the negative charges of the solid phase to the anions of the solution and vice versa. Soil particles and solid organic matter have a negative charge and thus can hold the cations; primarily calcium, magnesium, sodium, aluminum and hydrogen ions. Since the anion of greatest quantitative significance in soils is nitrate and it is almost exclusively in free solution, an equivalent concentration of cations must also be in solution (Epstein, 1972).

The primary nutritional problem for plants growing on saline soils is getting enough potassium, because sodium (and magnesium) compete with potassium for the same transport mechanism. The role of calcium ions is crucial. If enough calcium is present, a high affinity uptake system with preference for potassium can operate efficiently (Salisbury

& Ross, 1978; Greenway & Munns, 1980).

The role of sodium in plant metabolism has not been conclusively demonstrated. Clarkson and Hanson (1980) feel that sodium is not essential to any plants except certain salt tolerant plants with C_4 - metabolism and Crassulacean acid metabolism (CAM). Flowers et al (1977) have shown that growth of CAM and C_4 - metabolism plants is increased by micronutrient levels of sodium, suggesting that sodium is essential in these plants.

Various members of the milkweed family, Asclepiadaceae, utilize CAM acid metabolism (Waisel, 1972). These plants fix carbon dioxide at night since the stomata normally open in the dark and close in the light. Carbohydrate is converted to phosphoenol pyruvate (PEP) which is carboxylated to oxaloacetate and then reduced to malate (Krogmann, 1973). Perhaps this mechanism of accumulating organic acids is operating in Asclepias fascicularis and osmotically balances the accumulation of sodium.

The general response of vascular plants is to accumulate necessary ions from the soil when those ions are in low concentrations. Sodium is not known to be essential for non-halophytes, yet a previous study has shown accumulation of this ion in A. fascicularis growing in serpentine soil (Boyko, 1980).

The present study showed significant accumulation of sodium by both A. fascicularis and A. speciosa in both serpentine and non-serpentine soils. Sodium accumulation was actually greater in non-serpentine than serpentine soil (Table IV). Because Boyko's (1980) conclusion was based on a single sample, the results reported here probably represent the normal condition in these species.

There was no significant correlation between soil sodium and plant sodium in Asclepias fascicularis growing on non-serpentine soil ($r = -0.18$). However, in serpentine soil, the greater the soil sodium, the greater the degree of plant accumulation of the ion. This high correlation ($r = 0.80$) suggests that sodium may play a role in the survival of this species on serpentine soils. For example it might be used in place of, or in addition to, calcium to ameliorate the toxic effects of magnesium. However, this theory may be contradicted by the greater accumulation of sodium by plants growing on non-serpentine soils. It is possible that sodium is in some way actually required by some species of Asclepias and that plants living under the more stressful serpentine soil are unable to accumulate as much of this ion as on non-serpentine soil. Elucidation of the mechanisms is beyond the scope of this paper. The lack of correlation between soil and plant sodium concentrations in non-serpentine soils (Figure II) may simply reflect the fact that "non-serpentine" is not a specific soil type.

The exclusion of sodium in Asclepias cordifolia on non-serpentine soil is a more "typical" plant response to this ion. It is worth noting that the site from which A. cordifolia was collected happened to be volcanic soil with a sodium concentration almost three times higher than any other site. This clearly demonstrates that sodium accumulation is not a general characteristic of the genus Asclepias. A somewhat similar situation has been reported for the sodium-accumulating halophytic genus Atriplex in which sodium is essential for some, but not all, species (Brownell, 1967).

Variability in the physiological performances of plants is a function of their innate genetic constitution and their soil environment. Our knowledge of the extent and mechanisms of ion

accumulation and exclusion in Asclepias would be enhanced by examining the following questions:

1. How general is the phenomenon of sodium accumulation in Asclepias? Analysis of the native California species growing in various soil types could be performed.
2. Is sodium differentially accumulated by different parts of the plant? Analysis of specific plant parts (roots, stems, leaves, flowers and latex) could answer this question. Because some halophytes are known to store sodium in epidermal cells or glandular hairs, it would be interesting to analyze the hairs of those species which possess them. Information on differential accumulation might also be obtained with EDAX (electron dispersion analyzer using X-rays) which is available at San Joaquin Delta College. The rate of accumulation could be determined by collecting and analyzing plants collected at different stages of development.
3. Is sodium essential for growth in those species which accumulate it? The definitive answer to this question can come only from careful hydroponic growth of the plants in the absence of sodium. It is possible that micronutrient quantities of sodium may be necessary for normal growth.
4. Do the sodium-accumulating species of Asclepias have C_3, C_4 or Crassulacean acid metabolism? Synthesis of large quantities of organic acids at night would signify CAM - metabolism and suggest that accumulation of sodium might be necessary to maintain charge balance. An indirect

method of determining this might be to measure levels of organic acids in fresh plant tissue prepared after light and dark exposure.

SUMMARY

Three species of California native plants (*Asclepias fascicularis*, *A. speciosa* and *A. cordifolia*) and samples of the soil in which they were growing were collected from serpentine and non-serpentine areas. The sodium concentration in the aerial plant parts and in the soil was determined by atomic absorption.

This study showed significant accumulation of sodium by both *A. fascicularis* and *A. speciosa* in both serpentine and non-serpentine soils. *A. cordifolia* showed significant exclusion of sodium from non-serpentine soil. Plant sodium in non-serpentine sites was significantly higher than in serpentine sites for *A. fascicularis* but not *A. speciosa*. The concentration of sodium in *A. fascicularis* was correlated to the soil sodium concentration in serpentine soils but not in non-serpentine soils.

When analysis is restricted to soil sites with similar sodium concentrations there is no distinct pattern to plant sodium content. It is clear that the interaction between plant and soil is as complex and as diverse as the species and the environment in which it grows.

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Table I. Sodium concentrations (ppm/g dry weight) in plant tissues and in soil.

A. Asclepias fascicularis

Non-serpentine			Serpentine		
Site no.	Plant	Soil	Site no.	Plant	Soil
1	80	4.8	8	8.2	2.4
	116	5.6		6.2	2.2
	157	7.2		7.3	2.4
	156	5.8		11.6	3.4
	75	5.6		8.0	5.2
	99	5.4		7.8	1.6
2	41.6	14.6	9	11.2	5.8
	78.8	12.4		30.8	5.6
	40.4	12.6		15.8	7.2
	61.2	10.8		23.4	5.6
	70.4	11.8		17.0	5.6
	71.6	11.0		15.4	5.8
3	9.0	4.6	10	82	11.2
	33.3	3.6		55	12.0
	13.8	5.6		69	13.0
	50.0	3.4		64	10.2
	11.4	6.2		44	13.2
	33.4	4.8		83	11.8
4	11.6	5.2	11	9.6	5.2
	5.8	6.8		10.4	4.2
	13.4	7.2		13.3	7.8
	7.2	7.6		10.2	6.4
	14.8	5.0		6.6	2.6
	11.4	5.8		7.6	4.8
5	12.2	3.0	12,	22.2	5.8
	22.0	3.4		9.4	3.2
	20.0	3.4		21.6	3.4
	14.2	4.8		31.4	3.2
	20.2	4.8		7.6	2.8
	23.4	3.6		23.0	2.8
			13	6.6	3.4
				8.2	3.6
				11.0	5.0
				10.0	3.3
				20.2	6.2
				5.0	5.2

Table I (cont.)

A. Asclepias fascicularis (cont.)

Non-serpentine			Serpentine		
Site no.	Plant	Soil	Site no.	Plant	Soil
			14	16.8 13.2 15.2 34.0 22.4 22.4	5.8 5.8 5.0 6.2 5.2 5.2
$\bar{x} \pm S$	45.8 ± 42.7	6.6 ± 3.2		21.8 ± 20.4	5.6 ± 3.0

B. Asclepias speciosa

Non-serpentine			Serpentine		
Site no.	Plant	Soil	Site no.	Plant	Soil
6	8.0 8.0 4.4 5.4 19.4 12.2	3.8 3.0 3.6 3.6 2.8 4.2	15	7.2 7.4 6.0 13.6 30.8 11.8	6.2 6.2 6.2 6.2 6.2 5.8
$\bar{x} \pm S$	9.6 ± 5.5	3.5 ± 0.5		12.8 ± 9.3	6.1 ± 0.2

C. Asclepias cordifolia

Non-serpentine		
Site no.	Plant	Soil
7	6.0 6.4 5.6 4.6 4.8 7.4	17.8 32.8 34.6 27.8 34.4 31.2
$\bar{x} \pm S$	5.8 ± 1.0	29.8 ± 6.4

Table II. Comparison of plant sodium concentration to ranked soil sodium concentration in both serpentine (S) and non-serpentine (N-S) soils in three species of Asclepias.

*	Mean Soil ppm	Site no.	Mean Plant ppm	Soil type	Species
	2.9	8	8.3	S	A. fascicularis
	3.5	12	19.2	S	A. fascicularis
	3.5	6	9.6	NS	A. speciosa
	3.8	5	18.7	NS	A. fascicularis
	4.4	13	10.2	S	A. fascicularis
	4.7	3	25.1	NS	A. fascicularis
	5.2	11	9.7	S	A. fascicularis
	5.5	14	20.7	S	A. fascicularis
	5.7	1	114.0	NS	A. fascicularis
	5.9	9	18.9	S	A. fascicularis
	6.1	15	12.8	S	A. speciosa
	6.3	4	10.7	NS	A. fascicularis
	11.9	10	66.0	S	A. fascicularis
	12.2	2	60.7	NS	A. fascicularis
	29.8	7	5.8	NS	A. cordifolia

*Vertical bars indicate sites in which soil sodium was not significantly different when tested with the LSD test at the 0.1 level.

Table III. Mean, standard deviation (S.D.) and coefficient of variability (V) of soil and plant sodium (ppm/g dry weight) at each site.

A. Asclepias fascicularis

Site no.	Soil			Plant		
	Mean	S.D.	V	Mean	S.D.	V
	Non-serpentine					
1	5.7	0.80	14	114	36.1	32
2	12.2	1.40	11	60.7	16.2	27
3	4.7	1.09	23	25.1	16.3	65
4	6.3	1.09	17	10.7	3.51	33
5	3.8	0.65	17	18.7	4.47	24
	Serpentine					
8	2.9	1.28	44	8.3	1.78	21
9	5.9	0.63	11	18.9	7.02	37
10	11.9	1.12	9	66	15.3	23
11	5.2	1.18	35	9.7	2.51	26
12	3.5	1.14	33	19.2	9.04	47
13	4.4	1.21	28	10.2	5.38	53
14	5.5	0.47	9	20.7	7.54	36

B. Asclepias speciosa

Site no.	Soil			Plant		
	Mean	S.D.	V	Mean	S.D.	V
	Non-serpentine					
6	3.5	0.52	15	9.6	5.52	58
	Serpentine					
7	29.8	6.37	21	5.8	1.04	18

Table III (Cont.)

C. Asclepias cordifolia

Non-serpentine						
Site no.	Soil			Plant		
	Mean	S.D.	V	Mean	S.D.	V
15	6.1	0.16	3	16.7	11.2	67

Table IV. Student's t-test comparing mean sodium concentration in *Asclepias fascicularis*, *A. speciosa* and *A. cordifolia* in non-serpentine (N-S) and serpentine (S) soil.

Variables	Means		1- tailed probability
	Plant ppm	Soil ppp	
A. fascicularis S	21.9	5.6	0.000
A. fascicularis N-S	45.8	6.5	0.000
A. fascicularis S & N-S	31.8	6.0	0.000
A. speciosa S	16.7	6.1	0.034
A. speciosa N-S	9.6	3.5	0.024
A. speciosa S & N-S	13.2	9.2	0.003
A. cordifolia N-S	5.8	29.8	0.000

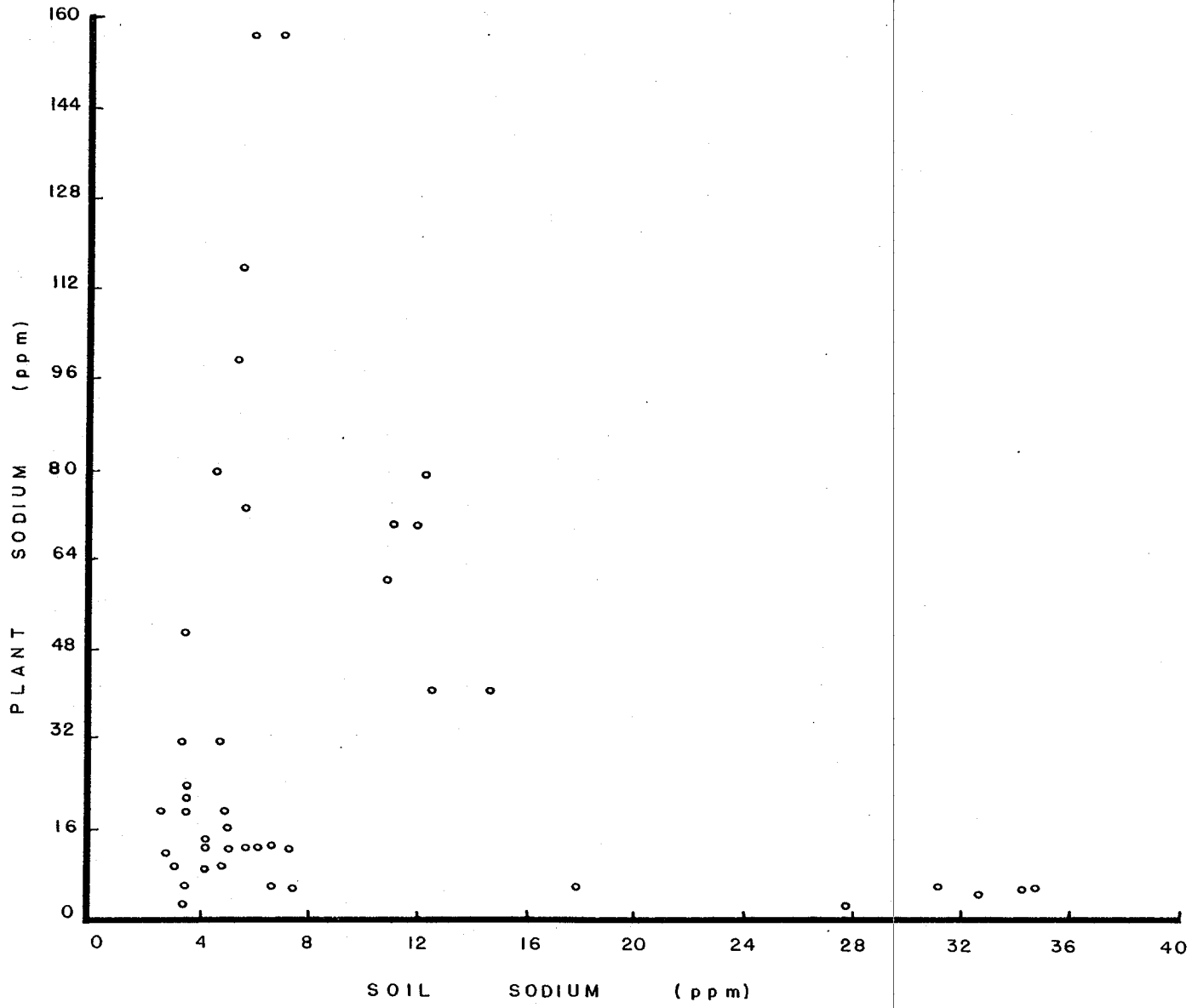

Figure 2. Relationship of plant sodium to soil sodium concentrations for A. fascicularis on non-serpentine soil (r = -0.18).

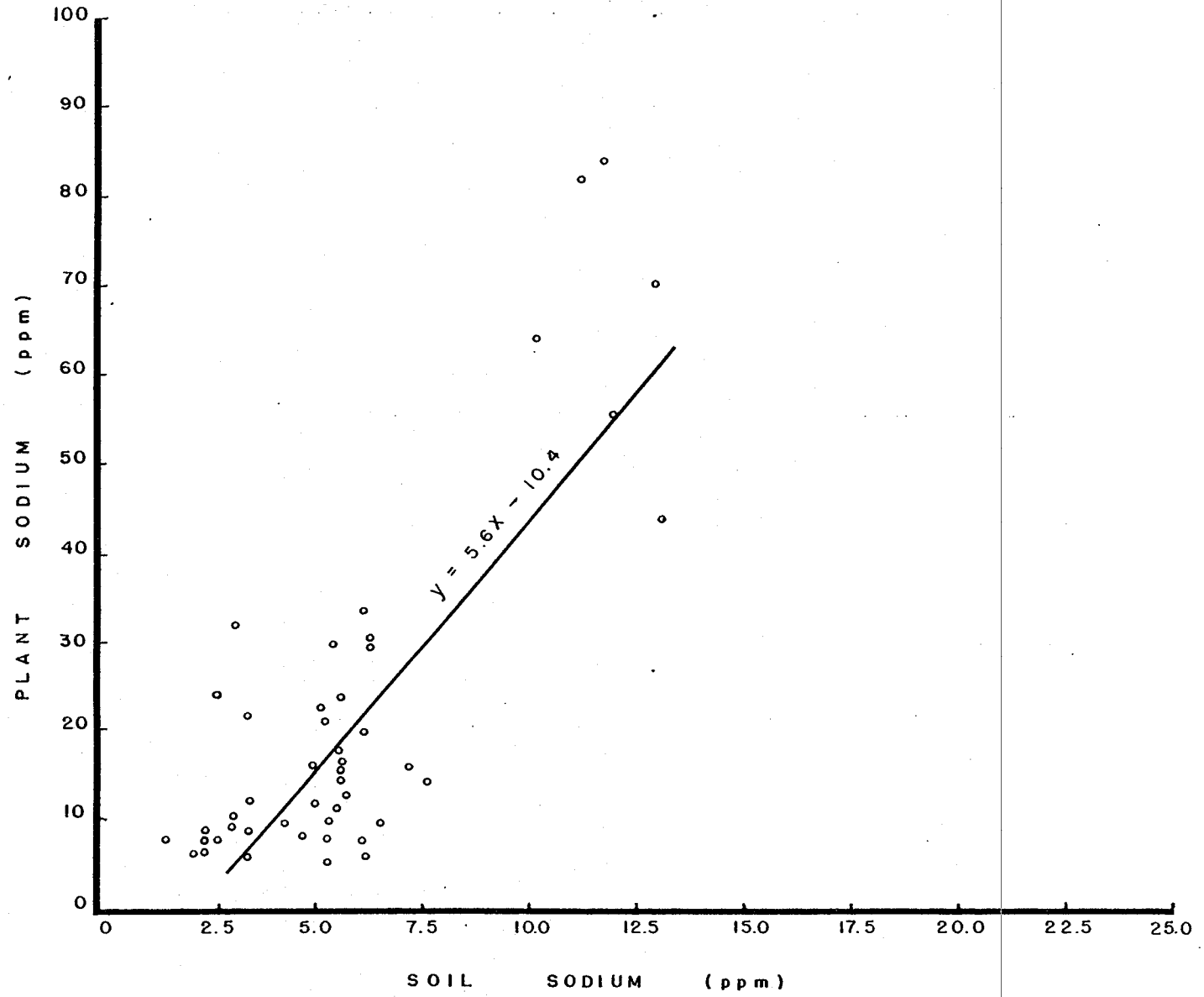

Figure 3. Relationship of plant sodium to soil sodium concentrations for A. fascicularis on serpentine soil (r = 0.80).

APPENDIX

Plant Species Studied

1. Asclepias fascicularis Dene, in A. DC. Milkweed. Herbaceous-perennial; the stems several, erect, 5-9 dm. tall, glaborous or sparsely puberulent; lvs. linear to linear-lanceolate, usually in whorls of 3-6, or lower and upper fewer, 4-12 cm. long, 3-10 mm wide, short-petioled, commonly folded midrib; umbels several in upper axils, many-fld; peduncles 2-5 cm. long; corolla greenish-white, often tinged purple, the lobes oblong, 4-5 mm. long; hoods ca. as long as stamens, broadly ovate; horns slender, exserted, incurved; follicles smooth, narrow, acuminate, 6-9 cm. long; seeds ca. 6 mm. long, the coma 3 or more cm. long. Frequent as colonies in dry places, mostly below 7,000 ft.

2. Asclepias speciosa Torr. Stout, Milkweed. Herbaceous, soft-tomentose or sometimes glabrate, the stem 5-12 dm. high, leafy to summit; lvs. opposite, oval to oblong, short-petioled, acute to obtuse at apex, rounded to cordate at base, 8-15 cm. long; umbels few, peduncled, the lower the fewer fls. than the many-fld terminal one; pedicels and calyx heavily tomentose, the former 1.5-3.5 cm. long, the latter 4-5 mm. long; corolla-lobes rose-purple, 8-10 mm. long, woolly on the back; hoods pinkish, aging yellowish, much longer than stamens, with wide involute base and then abruptly contracted into a nearly flat lance-shaped part; horns much exserted, incurved; follicles narrow-ovoid, densely woolly, 6-10 cm. long, scattered soft-spiny; seeds ca. 8 mm. long; 2n = 22 (Moore, 1946). Dry gravelly and stony places, mostly below 6,000 ft.

3. Asclepias cordifolia (Benth.) Jeps. Milkweed. Herbaceous, from a stout woody root, glaborous to somewhat puberulent; stems 3-8 dm. high, often tinged purple in upper parts; lvs. mostly opposite, ovate and mostly acute, cordate-clasping, 5-15 cm. long; umbels loosely many-fld., 1-several at apex and in upper axils, short peduncled; pedicels filiform, 1.5-3.5 cm. long; calyx-lobes purple, somewhat pubescent, 2.5-3 mm. long; corolla-lobes dark red-purple, 8-9 mm. long, oblong, glabrous, hoods purplish, short-cylindric, open at top and cleft down inner surface, truncate above and the inner angles produced into an ascending toothlike cusp; follicles lanceolate to oblong, straight, long-acuminate, 10-14 cm. long, glabrous; seeds 7-8 mm. long, the coma 2.5-3 cm. long. Open or wooded slopes, 500-6,300 ft.

(Munz, 1973)